DARWIN AND WALLACE ON SEXUAL SELECTION AND WARNING COLORATION

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IN looking over the life of Wallace recently, my attention was again drawn to the differences in opinion existing between Darwin and himself, with reference to sexual selection. Wallace objected to Darwin's assumption that a bright or peculiar color or a peculiar note or call would attract the attention of other individuals of the same species but of the opposite sex, on the ground that such a process could not become operative in forms which did not have sufficient intelligence to discriminate, and hence could not explain the occurrence of such characters in the lower forms. And if the plaint of the eugenists be accepted at its face value, the degree of intelligence even in the human subject to-day is not sufficient to insure discrimination in choosing a mate.

The development of our knowledge of animal behavior, on the one hand, and the advances in our knowledge of the nervous system, on the other, appear to me to make possible a reconsideration of the matter from the point of view of one or the other of these two lines of work at the present time. It must not be supposed that the approach from this angle will settle the question quite independently of other considerations, but such a method of approach may adduce some independent probability of the soundness or unsoundness of Darwin's point of view.

In the first place, sexual selection with reference to color of coat or plumage or of song is dependent upon the existence of a particular group of sense organs capable of perceiving objects at a distance—the distance receptors as Sherrington[1] calls them. These are the eye and the ear and the olfactory organ. The perception of color and voice depends therefore upon the development of the eye and the ear. Sexual selection with reference to these two characters can not be operative, therefore, in forms not able to see or hear.

It is evident that any other process of selection that is dependent upon coloration, even including protective coloration under certain conditions, must be considered from the same point of view. We may, therefore, discuss the subjects of colors of flowers as a means of attracting bees, warning coloration, protection by mimicry, and certain phases

[1] Sherrington, "Integrative Action of the Nervous System," New York, 1906.

of protective coloration in connection with sexual selection, since it is clear that the same objection, namely, the need of intelligence, may be urged against the assumption of warning coloration. And warning coloration is effective against some animals with distance receptors, but not necessarily against animals without such sense organs.

Visual and auditory mechanisms make their appearance well down in the animal scale, and hence the possibility of reactions through these mechanisms also arises rather low in the scale. The question then shifts to the central nervous system, and we must inquire whether in any of the lower forms, before the onset of intelligence, reactions to color are possible.

Since the work of Sumner[2] on the change of color pattern in flounders when placed in an aquarium with a certain color pattern in the bottom, we have known that reactions to color do occur under certain conditions. There are, of course, certain limitations to the process, and the mechanism of the response may still require investigation, but the response of the fish to visual impressions is undoubted, and it would be a far cry to postulate intelligence in the process. If a flounder responds to changes in the color pattern of the bottom of an aquarium, it is apparently not a more serious offense to postulate a response to a peculiar color pattern in another flounder. Other observations of the same kind on other animals lead to similar conclusions with regard to response to color. In the terminology of the physiologist, the response is a reflex process, involving an afferent or sensory impulse, the mediation of the central nervous system, and some efferent or outgoing nervous channel to the pigment cells of the skin. The medieval debate as to whether a reflex must always occur through the spinal cord, or even through the palæencephalon[3] is quite beside the point.

Another instance in which the appeal of color or odor is of importance is the attraction of bees and insects generally by flowers. The debate on the color vision of bees is far from closed, but that color plays some rôle will probably be admitted without prolonged argument. Whether bees have a sense of smell may perhaps be an open question, but that flowers attract bees seems clear. Both flower and insect visitor often have developed extraordinary modifications of the primitive type of structures so that neither insect nor flower can get along without the other. The yucca plant and the Pronuba moth constitute a case in point. Often but one species of insect can fertilize a particular flower, and it may happen that an insect can successfully visit but one species of flower. The question is not so much how the insect knows enough to visit that particular flower, but what particular features of the flower appeal to specific sense organs of the insect.

[2] Sumner, *Journal of Experimental Zoology*, 1911, X., pp. 409–479.
[3] Edinger, *Journal of Comparative Neurology*, 1908, XVIII., pp. 437–457.

In warning coloration or terrifying attitudes, nothing can be warned or terrified which does not see the warning or terrifying individual. The only question that arises is again whether the warned or terrified one must be possessed of sufficient intelligence to think the matter over and decide according to the evidence presented to it by the visual mechanism or whether it merely obeys the first impulse. Wallace himself proposed this theory of warning coloration, and it must stand or fall on purely theoretical grounds along with the theory of sexual selection, postulating, as it does, the same mechanisms in the warned individual that Darwin's hypothesis postulates in the attracted individual. There is, however, more direct observational evidence in favor of warning coloration than there is in favor of sexual selection. Birds, as Wallace showed, are warned by certain colors of butterflies.

Whitman's[4] observations on pigeons show that their responses and reactions are in many cases purely instinctive, being elicited without previous education or experience, and occur only when the group of conditions is right. Instinct, to me, at least, means a definite response to a definite group of afferent impulses. The afferent impulses once set up, the response of the central nervous system is the same under the same conditions. As Whitman expressed it, "organization shapes behavior," a statement directly in line with Hermann's law of specific response to stimulation. And from this statement of Whitman's dates the transition of the discussion of animal behavior in metaphysical terms to its discussion in terms of biological entities. In animal behavior, organization centers largely, though not wholly,[5] around the central nervous system and its associated afferent and efferent channels and sense organs. Internal secretions of various ductless glands of the body, and afferent nervous impulses from certain of these various glands are, of course, to be considered in animal behavior, and all of them have their influence on the instinctive responses of animals at various seasons of the year. Yet all these things are to be considered as a part of the organization of the individual at any one time. And the conviction is slowly growing, in my own mind, at least, that it is not so much a single afferent impulse as it is groups of afferent impulses that determine the reactions of animals. A few illustrations will make this point clearer.

Hunger has been shown to be associated with definitive movements of the stomach in man, and hence with definitive afferent impulses from the stomach.[5a] In the wider sense of the term, hunger is of reflex origin. The feeding reactions of the newly hatched *Necturus* are accurately and certainly elicited when the animal is hungry, as Whitman showed, but

[4] Whitman, "Animal Behavior," Marine Biological Lectures, 1898.

[5] Pike, *Quarterly Journal of Experimental Physiology*, 1913, VII., pp. 22–26.

[5a] Cannon, Harvey Lectures for 1911–12, pp. 130–152, Philadelphia.

not when the hunger is satisfied. There has been much debate as to why the animal no longer responds as well to the sight of food held in a certain position after its hunger is satisfied as before. It would seem sufficient to remember that the afferent impulses coming from a full stomach differ greatly from the afferent impulses coming from an empty one; and it is not, in my opinion, necessary to postulate a mysterious psychical change, of obscure origin, in the animal to explain its failure to take food after its hunger is satisfied. While all the external conditions may be the same, the afferent impulses from the stomach, and hence the group of afferent impulses concerned in the feeding response, is changed after hunger is satisfied. Two different groups of impulses, although they may have certain impulses in common, are not necessarily integrated to the same motor response.

The "Geschlechtstrieb" is similarly associated with a particular group of afferent impulses, dependent from their origin, among other things, upon changes in internal secretions, and changes in the circulatory conditions in particular local regions. A review of the various influences operative in exciting sexual desire of higher animals is found in a paper by von Bechterew,[6] and the argument need not be pursued at length here. Sufficient has been said to show that both the feeding and the sexual act have their driving force in particular groups of afferent impulses, some of which are of internal (proprioceptive or interoceptive) origin. The state of hunger or of sexual desire once established, the consummation of either the feeding or the sexual act is dependent upon external conditions which may be more or less fortuitous. The sight of food when the animal is hungry is an incitement to take food. If the sight of a peculiarly colored butterfly warns the bird, we will say, against taking it as food, we have the afferent impulses of internal and of external origin acting in opposition, and it will readily be seen that if the color of the butterfly is to protect it, that color must convey a very strong stimulus to the bird.

In the case of the sexual act, the conditions under which Darwin imagined that pleasing song or beauty of plumage might be operative are somewhat different. The female is ready for the sexual act, and awaits the coming of the male. To the internal stimuli, there may conceivably be added an external group in the nature of a color pattern that attracts her attention or a song that mingles with the mood or more properly, with the group of other afferent impulses, and the addition of these simple elements, not necessarily powerful in themselves, may be just sufficient to turn the balance in the favor of the male possessing them. In the case of warning coloration, the warning color must act as a powerful deterrent agent, but in the case of a bright plumage or a pleasing song, both external and internal stimuli work together.

[6] Bechterew, *Archiv für Physiologie* (Englemann's), 1905, p. 524.

Nor can it be held that warning coloration depends upon the intelligence of the warned individual. Certain mimic butterflies may have only a superficial resemblance to each other, but the resemblance is sufficiently close to save the mimic from attack by the animals which spare the mimicked forms. Birds are not close critics or students of certain types of color patterns. A more critical observer would not be so easily deceived.

These considerations are wholly independent of the origin of mimicry. Conceivably, there have been cases arising in nature in which one species has developed certain characters which render it unfit for food; and another species, which may develop a color pattern similar to that of the noxious form, has been spared because of this resemblance. But all cases of supposed mimicry are not necessarily of this sort. As Eigenmann[7] has shown, many cases which might, under other conditions, have passed for mimicry are really cases of convergent or parallel evolution, the similarities arising from similar responses of different organisms to the same or similar features of the environment. Indeed, Eigenmann's position seems especially strong, since he is able to supplant the hypothesis of mimicry, wherever it is weak, by the more general theory of natural selection. But the essential point to be kept in mind in this connection is that, no matter how the resemblances may have arisen, if mimicry protects at all, the mimic escapes because of the lack of a keenly critical faculty in the pursuer.

An animal of a low grade of intelligence is more apt to show uniformity of deportment than an animal of a higher grade. The frog has never rivaled either the serpent's or the owl's reputation, possibly undeserved, for wisdom, but it reacts to a red rag with avidity. A really intelligent animal would not be so easily humbugged. A contraption of feathers, gay colors and steel wire will lure a trout from his pool, often to his sorrow, but the deception in the hands of competent deceivers proceeds from year to year. Any skillful angler will verify the statement that it is the trifling things which are of importance in the pursuit of fish. The catfish is more prosaic and demands more of the reality in the form of worms, not being satisfied with the mere semblance of food.

The arguments which apply to warning coloration apply equally well to sexual selection, and it is clear from what has been said that neither sexual selection nor warning coloration require any great amount of intelligence on the part of the warned individuals or the pleased ones. Indeed, it is conceivable that both processes might act more strongly in animals which were not too intelligent. In man, financial, social and family considerations often outweigh the more natural considerations.

[7] Eigenmann, *Annals of the Carnegie Museum*, 1909–10, VI., pp. 4–54, and later papers.

Arguments of this kind can not, of course, lead to a definite settlement of the question of the potency of sexual selection, but they appear to increase the probability that sexual selection may be a reality, and a more potent agent in evolution than we have realized or been inclined to admit. Many peculiar characters have a function that is at present unknown, and many of these unknowns have been supposed to act as factors in sexual selection. More accurate observation has, however, shown their true use in the animal's activities. The horns of the *Orocytes rhinoceros,* recently described by Doane[8] afford an example of a character, once supposed to be effective in sexual selection, which has proved to be of direct use to the animal in getting its food, and hence, an agent in natural selection. Undoubtedly, further studies of animals and plants in their natural environment will lead to still further instances in which characters apparently useless, so far as their relation to getting food or resisting enemies goes, will prove to have some direct use in the life of the animal or plant. Even at present, characters supposed to be active through sexual selection alone should be scrutinized with some care before their case is admitted to serious consideration.

The view that the secondary sexual characters are the expression of internal metabolic changes, internal secretions, and the like, does not exclude a selective value. Darwin did not explain the origin of such variations, but supposed that they might be of selective value, and if secondary sexual characters are related to the activity of organs of internal secretion, such an occurrence need not disturb us. Physiologists generally regard all an organism's responses as due to an interaction of internal and external factors, and some such similar relationship is probably at the bottom of orthogenesis. As I hope to point out in a later paper, there is much evidence of a chemical nature in favor of orthogenesis.

It is true that external characters or purely morphological characters such as muscles and bones have, heretofore, formed the greater part of the subject matter of discussions on evolution. But the idea of the potency of internal functional factors in evolution has crept in, and Gaskell has pointed out that two general kinds of mechanisms of internal coordination—the nervous and the chemical—have been concerned in evolution. Both kinds of mechanisms are of selective value. Regarding lactation as a secondary sexual character, great changes in such a character, dependent partly upon morphological, but largely upon chemical organization, have been brought about in the various breeds of dairy cattle by artificial selection. And in this domain of the heredity of chemical characteristics lies a whole field of experiment on characters susceptible of accurate quantitative measurement as yet barely touched by the hand of the Mendelian.

[8] *Science,* 1913, N. S., XXXVIII., p. 883.

It is a truth that loses none of its force by repetition that in laboratory observation of animals, the laboratory conditions do not always accurately represent the conditions in nature, and that the deportment of an animal in the laboratory may not be exactly the same as its deportment in nature. The failure of some relatively high animals to breed in captivity is a case in point, and this again calls attention to the importance of a group of afferent impulses rather than a single impulse in determining the response of animals. Some subtle influence of the natural environment is lacking in the conditions obtaining in captivity, and the normal deportment of the animals is modified in at least one important detail. Other animals have a nervous system of sufficient plasticity to adjust themselves to the changed conditions of the laboratory or zoological garden. But the laboratory experimenter is now, and will be for some time to come, dependent upon the data of close and accurate observers of animal life in the field for his basis of comparison. And until the laboratory worker is certain that the deportment observed in the laboratory corresponds to that in nature, his analysis is not biologically accurate.

It is probably true, as Professor Cockerell[9] suggests, that no man will ever be able accurately to tell the complete story of Wallace's life work, even on its biological side alone, using the word in its widest sense. It is an evidence of the genius of Darwin and of Wallace that each was able to get such a fundamental grasp of the phenomena of nature as to afford problems for workers in other lines apparently far removed from their own. The experimental physiologist has had relatively little to say in regard to evolution as yet, and is perhaps in no position to settle dogmatically any particular problem now. But physiology has a direct contribution of interest to the worker in certain phases of a much wider problem. Specialties multiply, new and confusing terminologies develop, and the point of view ever tends to become narrow. Biologists pursuing one specialty have more and more difficulty in communicating to biologists in other lines of work, the particular results in their own. And biologists are almost unintelligible to workers in physics and chemistry. Yet science is a unit, and there can be no lasting truth developed in one field unless it is in accord with truth in every other field. The task of finding out what other workers have to offer us is a huge and even insuperable one under present conditions. Some hope of relief may be held out when the biologists get some of their great generalizations reduced to simpler form, and consequently intelligible to the scientific multitude. At present, the theory of evolution seems to be the most promising common meeting place to which biologists in all lines of work may bring their contributions for the judgment and criticism of their brother workers.

[9] *Science*, 1913, N. S., XXXVIII., p. 871.

In fact, it seems as if Darwin and Wallace, Nägeli, Haeckel, Dohrn, Weismann, De Vries and a host of other investigators, had grappled with an all-embracing problem—a problem of problems that must engage the best energies of all the sciences for centuries yet to come.[10]

It is a striking evidence of the slight degree to which our subjects have been developed that we are so often blind to the general implications of our work, and the need for help from every conceivable quarter was never greater than now. The opportunity to acknowledge the influence of the great group of English biologists—Darwin, Huxley and Wallace, who showed that evolution of some kind and through some agency was a fact—upon my own line of work in an apparently distantly related field is a particularly grateful one. And it is more in the hope of directing attention to the tremendous breadth of the problem than of emphasizing any particular views of my own that this article is written. And if what I say may direct the attention of any other worker, in an apparently far removed and exceedingly specialized line, to what he may have to offer on the great problem of evolution in general, it will be well.

[10] Whitman, *Bulletin of the Wisconsin Natural History Society*, New Series, 1907, V., p. 6.